

AperTO - Archivio Istituzionale Open Access dell'Università di Torino

## Effects of the lack of forest management on spatio-temporal dynamics of a subalpine *Pinus cembra* forest

### This is the author's manuscript

*Original Citation:*

*Availability:*

This version is available <http://hdl.handle.net/2318/1582227> since 2018-03-27T13:23:08Z

*Published version:*

DOI:10.1080/02827581.2016.1207802

*Terms of use:*

Open Access

Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)

## Effects of the lack of forest management on spatio-temporal dynamics of a subalpine *Pinus cembra* forest

Journal:	<i>Scandinavian Journal of Forest Research</i>
Manuscript ID	SFOR-2015-0165.R2
Manuscript Type:	Research Article
Date Submitted by the Author:	27-Apr-2016
Complete List of Authors:	Giammarchi, Francesco; Free University of Bozen, Faculty of Science and Technology Vacchiano, Giorgio; Università degli Studi di Torino, Dipartimento di Scienze Agrarie, Forestali e Alimentari Bertagnolli, Andrea; Magnifica Comunità di Fiemme, Ventura, Maurizio; Free University of Bozen, Faculty of Science and Technology Panzacchi, Pietro; Free University of Bozen, Faculty of Science and Technology Cherubini, Paolo; WSL, Swiss Federal Research Institute, Tonon, Giustino; Free University of Bozen, Faculty of Science and Technology; MountFor Project Centre, European Forest Institute,
Keywords:	Forest dynamics, Spatial patterns, Dendroecology, Growth dominance

SCHOLARONE™  
Manuscripts

Effects of the lack of forest management on spatio-temporal dynamics of a subalpine *Pinus cembra* forest

GIAMMARCHI Francesco<sup>1</sup>; VACCHIANO Giorgio<sup>2</sup>; BERTAGNOLLI Andrea<sup>3</sup>; VENTURA Maurizio<sup>1</sup>; PANZACCHI Pietro<sup>1</sup>, CHERUBINI Paolo<sup>4</sup>; TONON Giustino<sup>1,5</sup>.

<sup>1</sup> Faculty of Science and Technology, Free University of Bolzano, Piazza Università 5, 39100 Bolzano, Italy.

<sup>2</sup> Dipartimento di Scienze Agrarie, Forestali e Alimentari, Università degli Studi di Torino, Via L. da Vinci 44, 10095 Grugliasco (TO), Italy.

<sup>3</sup> Magnifica Comunità di Fiemme, Viale Libertà 1, 38033 Cavalese (TN), Italy.

<sup>4</sup> WSL, Swiss Federal Research Institute, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland.

<sup>5</sup> MountFor Project Centre, European Forest Institute, Via E. Mach 1, 38010 San Michele a/Adige (TN), Italy.

Keywords: Forest dynamics, Spatial patterns, Dendroecology, Growth dominance

Abstract

Knowledge about the stand structure and dynamics of subalpine forests is crucial to preserve their multifunctionality. In the present study, we reconstructed the spatio-temporal dynamics of a subalpine *Pinus cembra* forest in the eastern Italian Alps in response to natural disturbances and forest management. We adopted a concurrent point pattern, dendroecological and growth dominance analysis. We mapped and measured all trees of *Pinus cembra* and *Larix decidua* in a 1 ha plot. We analyzed intra- and inter-specific spatial patterns and spatial autocorrelation of tree size and age. We explored establishment dynamics and shifts in competition by analyzing growth suppression/release patterns and growth dominance trends. Results showed a clumped, uneven-aged, multi-layered structure where pine was dominant. The synergic action of ecological and human-induced factors is discussed to explain the prevalence of pine over time. Spatial pattern and autocorrelation analyses suggest a different colonization strategy of the two species, in which pine established after small-scale perturbations and experienced a stronger inter- and intra-specific competition. The interruption of tree establishment and shift in growth dominance towards large trees resulting from the lack of forest management is the most important finding of this research. This highlights the importance of an active management to avoid a homogenization of the forest structure that is generally associated with a reduction of biodiversity and protective ability of forests.

## 31 Introduction

32 Swiss stone pine (*Pinus cembra* L.) and mixed pine – larch (*Larix decidua* Mill.) forests are typical ecosystems of  
33 the subalpine belt of the Alps, where they often build up the timberline (Risch et al. 2003), establishing with  
34 harsh environmental conditions such as mean annual temperatures ranging from 1°C to 5°C, minimum  
35 temperatures reaching -25°C and snow cover and frozen soil lasting trough the beginning of the growing  
36 season (Tranquillini 1979). These two species have complementary life traits and hence their distribution and  
37 mixture depend on the growth conditions they experience. Larch is a light-demanding, wind-dispersed species,  
38 whose regeneration takes advantage of disturbances that expose mineral soil (Schloeth 1998), and thus can be  
39 considered a pioneer species. By contrast, stone pine is a shade-tolerant species, achieving dominance in mid-  
40 and late-successive subalpine forests (Krüsi and Moser 2000). Its heavy seeds are mainly dispersed by the  
41 European thickbilled nutcracker (*Nucifraga caryocatactes* L.) and regeneration can also take place on soil  
42 covered by litter or grass.

43  
44 In absence of human influence, the main drivers of species composition and growth of the larch-stone pine  
45 subalpine forests are summer temperatures (Pfeifer et al. 2005; Tinner and Kaltenrieder 2005; Casalegno et al.  
46 2010), snow cover (Frey 1983), microtopography (Schönenberger 1985; Holtmeier 2009) and natural  
47 disturbances. These latter are usually characterized by high-frequency (seasonal to yearly), low- to mid-  
48 severity events, such as avalanches, rockfall, or larch budmoth (*Zeiraphera griseana* Hubner) outbreaks  
49 (Baltensweiler 1964; Nola et al. 2006). The occurrence of major disturbances such as fires or bark beetle  
50 outbreaks (Veblen et al. 1994) has been ascertained, starting from the mid Holocene (Blarquez et al. 2010), but  
51 their role in regulating species composition is uncertain and seemingly variable between sites (Genries et al.  
52 2009). In the past, the influence of climate and natural disturbances have been obfuscated by the human  
53 impact, such as livestock grazing and tree cutting. Starting from the 20<sup>th</sup> century, because of the depopulation  
54 of mountain areas and the adoption of more conservative forestry systems, natural factors have returned to  
55 be the predominant drivers of forest dynamics (Motta and Lingua 2005), especially at higher altitudes (Lingua  
56 et al. 2008).

57  
58 Currently, forest management at the timberline presents the challenge of preserving long-term ecological  
59 integrity and supplying environmental services (Dorren et al. 2004) in face of the extreme climate, peculiar soil  
60 and geo-morphological conditions and high frequency of disturbances. Therefore, knowledge of the stand  
61 structure and dynamics of high-elevation forests in response to the abovementioned drivers is crucial for their  
62 sustainable management, for instance to maintain their protective function (Brang et al. 2006). However, few  
63 monitoring experiments have been set up in Alpine high-elevation forest ecosystems (Wunder et al. 2008), and  
64 they generally lack sufficient timespan, if compared to the temporal length of these forests dynamics. To this  
65 end, evidence of past dynamics and response to perturbations can be inferred by retrospective analyses.  
66 Among these, dendroecological techniques aimed at dating past increases (releases) and/or decreases  
67 (suppressions) of tree growth (Rubino and McCarthy 2004) can provide important information on the dynamic  
68 response of forests to perturbations (Camarero et al. 2000), especially when this analysis is associated with the

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

study of spatial distribution of trees. In this context, spatial pattern distribution can be seen as the result of the interaction between establishment dynamics, intra- and inter-specific competition, past climate, type of disturbances and forest management (Moeur 1993; Dale 1999; Tonon et al. 2005).

In light of the previous considerations, the aims of the present study were: (1) to analyze the current spatial patterns of trees in a high-elevation Swiss stone pine forest of the Eastern Italian Alps, focusing on inter-specific (larch vs. pine) and inter-size (small vs. large trees) spatial relationships; (2) to reconstruct the process of forest establishment and (3) infer, by a concurrent dendroecological analysis of tree age, release/suppression events and growth dominance, which past natural and anthropogenic drivers brought to the current forest structure.

**Materials and methods**

**Study site**

The study area is located in the Natura 2000 site IT3120128 “Alta Val di Stava” (TN, Italy) (46°19’79”N, 11°32’26”E). The 1775 ha site, at an average elevation of 1840 m a.s.l. (max. 2345 m a.s.l., min. 1249 m a.s.l.), is dominated by coniferous woodlands (52%); subalpine scrub, alpine grasslands, and rocks that cover about 15% of total land area. The most common forest habitats are acidophilus Norway spruce (*Picea abies* (L.) Karst.) stands in the mountain belt (15% of total land area), and mixed European larch-Swiss stone pine stands (36%) in the subalpine belt up to the treeline, at about 2200 m a.s.l. (coded 9420 and 9410, respectively, by the EU Habitat Directive 92/43/EEC). The area was a grazed woodland during the 18<sup>th</sup> and 19<sup>th</sup> century (Ridolfi 2009). The abandonment of the traditional silvo-pastoral system reportedly occurred at the beginning of 20<sup>th</sup> century, except for the flat highlands that are still presently managed as pastures (Provincia Autonoma di Trento 2013). We selected a patch of European larch-Swiss stone pine forest at an elevation of 1860 m a.s.l., and in 2009 we established a permanent 100x100 m plot in which we carried out our study. The plot is dominated by Swiss stone pine with a minor presence of European larch and few trees of European rowan (*Sorbus aucuparia* L.) and Norway spruce (*Picea abies* Karst.). The understory is composed by a thick layer of *Rhododendron ferrugineum* L., *Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L. Average slope angle is 25° with a NNE aspect. Mean temperature is 3.9 °C (mean minimum temperature: -15 °C; mean maximum temperature: 23 °C) and the cumulated mean annual precipitation is 1100 mm (Passo Lavazè meteorological station). The parent material is limestone. Due to its nontrivial slope, it is unsure whether the study area has ever been managed as a pasture. In the Trento province, all public forests have been subject to management plans since 1954 (Ferrari 1988), based on close-to-nature silvicultural criteria (Wolynski et al. 2009). In particular, the forest under scrutiny was managed by selection cutting until 1966, when a mudflow permanently damaged the nearby forest road and active management ceased (Ridolfi 2009).

**Field sampling and tree mapping**

Within the plot, all living trees were mapped on a Cartesian coordinate system by a total station (Leica, UK), permanently tagged, and measured for species, stem height and stem diameter. The diameter was measured

at 130 cm height for large trees (diameter at breast height [dbh]  $\geq 7.5$ ) and at the root collar (rcd) for small trees (dbh < 7.5 cm). Additionally, two 33x100 m perpendicular transects were delimited (55% of the plot area), crossing the center of the plot. Within the transects, an increment core was taken at 80 cm height from both large and small trees, parallel to slope in order to avoid sampling compression wood and obtaining biased measurements (Cook and Kairiukstis 1990). Coring height was chosen to maximize the accuracy of true age estimates, while avoiding the most asymmetric part of the basal stem. A total of 229 large trees of pine and 31 large trees of larch were sampled, i.e., 47% and 49% of all the respective large trees in the plot. Concerning small trees, 55 pines and 10 larches were sampled, corresponding to the 24% and 20% of each species in the whole plot. In order to compute the mean age difference between stem base and 80 cm height, we cut 10 Swiss stone pine and 10 European larch small trees outside the experimental area. From each felled stem, we collected a cross-section at the stem base and at 80 cm and counted tree rings. The difference between the mean ring counts at collar and at 80 cm height were subsequently added to ring counts at coring height, in order to obtain a corrected estimate of tree age (Motta and Lingua 2005). Given the exploratory nature of the study and being ~~it~~ a beginning step for advanced studies, the statistical analyses used in this paper are generally basic if compared to more up to date techniques (Druckenbrod 2005, Ise and Moorcroft 2008, Renshaw 2010, Shimatani et al. 2011).

#### Dendroecological analysis

Following tree cores preparation by sanding with increasingly graded sandpaper, tree-ring width and number were measured by means of a LINTAB6 station and TSAP-Win software (Rinntech, Heidelberg). Individual tree-ring series were cross-dated and standardized using a negative exponential curve (Fritts et al. 1969) to remove age-related trends while preserving growth fluctuation related to past disturbances (Fritts 1976; Cook and Kairiukstis 1990). Standardization was performed through the ARSTAN package (Cook 1985). In order to identify past disturbance periods, radial growth release and suppression analysis (Lorimer 1985; Motta et al. 1999) was performed on 25 detrended tree-ring series of Swiss stone pine and 25 of European larch, evenly distributed in the two transect areas (Fig. 1). Only the oldest 25 trees available for each species were selected in order to have a broader time span while avoiding a huge unbalance in the size sample before and after the period of major establishment, bias that would have took place if we started to include younger trees. After computing 5-year running median segments starting from the first recorded year for each species (segment 1753-1757 for Swiss stone pine; segment 1830-1834 for European larch), we identified a release when the 5-year median growth was  $\geq 50\%$  of the median of the previous five years, and a suppression if it was  $\leq 50\%$ . Median values were chosen instead of simple average as they better represent the non-normality of tree-growth patterns (Rubino and McCarthy 2004). Release and suppression data were expressed as the percentage of trees showing release/suppression among the total number of trees analyzed in each 5-year period.

#### Point pattern analysis

Several methods have been proposed to describe point pattern spatial patterns (Diggle 1983). The main aim of these methodologies is to assess whether trees have a random, regular or clumped spatial distribution, in

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

order to infer the nature, intensity and duration of processes that may have originated the observed spatial structure (Diggle 1983; Camarero et al. 2000; Tonon et al. 2005). For this purpose, both a second-order analysis based on Ripley's K function (Ripley 1977), which calculates the variance of the distance between all possible point pairs within a given bi-dimensional space with a radius  $d$  (Duncan 1991), and the refined nearest-neighbour Diggle's G function (Diggle 1983), which is based on the distance between the event of a sample and its nearest neighbour, were computed for all the trees of the plot. Ripley's K was linearized by a square root transformation to  $L(d)$ , that has an expected value of zero under a Poisson distribution (Ripley 1979; Moeur 1993; Haase 1995). Obtained spatial patterns can be described, at any distance, as significantly clumped, regular or random when  $L(d)$  or  $G(w)$  are respectively higher, lower, or within a given quantile bound generated by  $n$  randomized iterations of tree positions within the plot. Both univariate analyses were carried out on all trees pooled, and separately on each species (Swiss stone pine, European larch) and size class (large and small trees), under the complete spatial randomness (CSR) null hypothesis, by using a Monte Carlo 99% confidence interval. Bivariate analyses were performed to assess the spatial relationship between large and small trees of stone pine ( $N = 481$  and  $224$ , respectively) and larch ( $N = 63$  and  $49$ ). We used Ripley's  $K_{12}$  function (Lotwick and Silverman 1982; Diggle 1983) in its square root transformation  $L_{12}(d)$ , and its non-cumulative equivalent Neighborhood Density Function (NDF) (Condit et al. 2000). Values of  $L_{12}(d)$  or Relative Neighborhood density greater, lower or within a Monte Carlo 99% confidence interval respectively indicate positive association (attraction), negative association (repulsion) or spatial independence between the two analyzed populations. A CSR null hypothesis for the two populations was assumed. All point pattern functions were computed by the SpPack Excel add-in (Perry 2004), with a distance lag of 1 m, generating 499 Monte Carlo simulations of tree locations and applying a toroidal edge correction for Ripley's K (Bailey and Gatrell 1995; Haase 1995) and edge correction (Gignoux et al. 1999) for Diggle's G and Neighborhood Density Function. The distance range was reduced from 1-15 m to 1-5 m because in the last 10 m no evident change was ever detected. Moreover, given the establishment in small groups typical of such forests, it is normal that most of the interactions are taking place in the first meters. Finally, spatial autocorrelation of tree height, diameter and age was calculated for all trees, and for large and small trees separately, by means of non-cumulative Moran's I index (Moran 1950), which ranges from -1 (negative autocorrelation) to 1 (positive autocorrelation), zero indicating absence of spatial autocorrelation (Fortin et al. 2002). Moran's I was also computed by the SpPack Excel add-in (Perry 2004), up to a distance of 5 m with a lag of 1 m, and tested for significance at each distance. All-directional spatial correlograms were computed for sets with 10 or more pairs of points available at all distances (Tonon et al. 2005), and tested for significance ( $P < 0.05$ ), using the Bonferroni procedure to correct for the dependence among the autocorrelation coefficients calculated for each distance. Given that age data were available only in the two perpendicular transects, Moran's I for this parameter was calculated only on a subsample of the population.

**Growth dominance**

In order to assess past changes in competitive environment, we used tree-ring data from the two transects to compute the temporal trend of stand growth dominance. Growth dominance relates the distribution of



growth rates of individual trees within a stand to tree sizes (Binkley et al. 2003). According to Binkley (2004), stand development entails a systematic change in the growth dominance of stands, articulated in four distinct stages. For each year  $m$  since the establishment of the oldest large tree, we used radial increments to back-calculate the dbh of each large tree, its volume using dbh-volume equations (Scrinzi et al. 2010), and its volume increment as the difference between volume in year  $m$  and volume in year  $m-1$ . We chose the appropriate site index for volume equations by computing average height at 100 years of all cored Swiss stone pines. Subsequently, we plotted cumulative increment vs. cumulative volume of trees arranged from the smallest to the largest one for each year (i.e., a growth dominance curve), and computed a growth dominance coefficient GD (Fernández et al. 2011) to quantify dominance level in each year:

$$GD = \frac{\sum_{i=1}^{n-1} Pv_i - Pc_i}{\sum_{i=1}^{n-1} Pv_i}$$

where  $Pv_i$  is the cumulative stem volume up to the  $i$ -th individual in relation to total stem volume, and  $Pc_i$  is the cumulative volume increment up to the  $i$ -th individual in relation to total volume increment. The growth dominance curve would follow a 1:1 line if the proportional contributions of each size class of trees were the same for volume as for volume increment. If larger trees accounted for a greater proportion of increment than for stand volume (positive dominance), the stand dominance curve would fall below the 1:1 line ( $GD > 0$ ). Stands where relatively low growth rates of larger trees account for a smaller portion of total stand increment than of stand volume, would show a “reverse” growth dominance (curve above the 1:1 line,  $GD < 0$ ) (Fernández et al. 2011): the large, structurally dominant trees would not dominate the growth of the stand. Since in the first half of the chronology the sample size was small and no information was available on the former stand structure, we chose to compute the GD index only starting from the 1920.

## Results

### Species composition and size-structure

The stand had a density of 593 large trees and 371 small trees per hectare and a basal area of  $36.55 \text{ m}^2 \text{ ha}^{-1}$ . *Pinus cembra* was the dominant species for both number of large trees and basal area (81% and 86% respectively), followed by European larch (11% and 9% respectively) (Tab. 1). European rowan and Norway spruce were rarer, constituting only the 6% and 2% of the large trees group (Tab. 1). Dominant height and mean diameter were 18,58 m and 27,63 cm respectively (Tab. 1). Distribution of diameters approximated a negative exponential curve typical of uneven-aged subalpine forests (Meyer 1943), with a large number of small trees and progressively decreasing with increasing size class (Fig. 2a). Pine was represented in almost all diameter classes up to the largest (90 cm). Larch occurred both in small and large diameter classes with the same proportion (Fig. 2a). The height distribution of large trees showed a bell-shaped curve with a maximum at 12-15 m, whereas small trees are almost completely grouped in the first 3 m class (Fig. 2b).



1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

**Age-structure, growth release/suppression and growth dominance analyses**

The mean length of site chronologies was 256 years (1753-2009) and 179 years (1830-2009) for Swiss stone pine and European larch, respectively. Average tree-ring width was 1.05 mm (max. width 2.10 mm; min. width 0.25 mm) for Swiss stone pine and 1.04 mm (max. width 2.05 mm; min. width 0.13 mm) for European larch. When apportioned into 5-year periods, age-structure showed a bell-shaped curve (Fig. 3). Most of the current large trees established between years 1845 and 1935, with a peak from 1900 to 1910. While pine was found in all age classes, larch was only sporadically present before 1900. After a peak of natural regeneration in the second half of the 1950 decade, no Swiss stone pine established after the 1970 (age of the youngest living small tree), and no European larch after 1975. A visual assessment of the release/suppression analysis results, showed regular shifts with a periodicity of about 20-25 years for Swiss stone pine, especially in the earlier part of the time series (Fig. 4). Two periods of growth release of Swiss stone pine occurred at the end of the 19<sup>th</sup> century and at the beginning of the 20<sup>th</sup>, and coincide with the observed strong establishment of this species. Moreover, a marked event occurred in the 1950 decade, causing a strong suppression of larch growth and a simultaneous release of Swiss stone pine, followed by an inverse reaction of both species. With the exception of these events, growth releases and suppressions never show a frequency higher than  $\pm 30\%$  throughout the 20<sup>th</sup> century. Results from the growth dominance analysis showed that it was always reversed ( $<0$ ). GD values were decreasing from 1920 until a minimum in the 1950, pointing to an increasingly consistent role of small trees in biomass production. However, from this minimum to 2010, GD increased meaning that small trees biomass production constantly decreased in favor of large trees (Fig. 5).

**Spatial distribution of trees**

Univariate point pattern analysis showed a clear tendency towards clumping of large trees of the investigated species (all species individually and combined) at all considered distances (Fig. 6a, 6c, 6e). Swiss stone pine  $L(d)$  peaked at 1 m distance, farther in larch. Small trees exhibited clumping at all distances, with higher aggregation in the first meters for *Pinus cembra*. These results were confirmed also by Diggle's G function, as  $G(w)$  values showed aggregation at all considered distances for small trees, both combined and separately (Fig. 7b, 7d, 7f), as well as aggregation for large trees at least until 3 meters (Fig. 7a, 7c, 7e). For what concerns  $L_{12}(d)$  bivariate point pattern analysis, large trees vs. small trees of both species combined showed spatial attraction for all distance lags (Fig. 8a). Intra-specific patterns, according to  $L_{12}(d)$ , exhibited continuous spatial attraction for pine and from 3 m to 5 m for larch (Fig. 8b, 8c), whereas inter-specific patterns showed random distribution between pine and larch large trees (Fig. 8d) and a significant attraction between Swiss stone pine and European larch small trees (Fig. 8e). Similarly, the non-cumulative bivariate point pattern analysis (NDF), showed attraction in the first and fourth lag between large and small trees of both species combined (Fig. 9a), as well as intra-specific attraction up to 2 m for pine (Fig. 9b) and from 3 to 5 m for larch (Fig. 9c). A random spatial distribution was observed between pine and larch large trees (Fig. 9d) and significant attraction between small trees of the same species (Fig. 9e). Correlograms (all species pooled) showed significantly

positive ( $P < 0.05$ ) autocorrelation of diameter in the first meter in large trees, and up to 2 m in small trees (Fig. 10a). Positive autocorrelation was detected at all distances for large trees height and at 1, 2 and 5 m for small trees (Fig. 10b). For large trees only, age was positively autocorrelated (Fig. 10c), diameter was positively autocorrelated only for pine at 2 m (Fig. 10d), whereas height was at 1 m for larch and from 2 m to 5 m for pine (Fig. 10e). Age was positively autocorrelated only for large trees of pine (Fig. 10f). Significant and positive autocorrelation of both diameter and height was detected in the small trees layer of Swiss stone pine at almost all distances, whereas larch was never autocorrelated, set aside from height at 5 m (Fig. 10g, 10h). Unlike large trees, significant age autocorrelation was discernible in small trees only at 2 m for larch and 4 m for pine (Fig. 10i).

## Discussion

Unlike previous studies on Alpine treeline forests, which were focused on mixed pine-larch woods (Carrer and Urbinati 2001; Motta and Lingua 2005; Lingua et al. 2008), the present study considers a stand clearly dominated by Swiss stone pine. Past disturbance regime, land-use, and microclimate conditions seem to have favored Swiss stone pine over European larch in the past. Historically, in grazable Alpine woodlands pine was generally removed whereas larch was promoted by landowners because of its lighter crown, suitable for the growth of the herbaceous layer (Garbarino et al. 2011). Nevertheless, age structure analysis showed that the oldest living trees are pines and almost no larch trees are dating back to a period prior to the end of the 19<sup>th</sup> century (Fig. 3). This suggests that the stand had only marginal grazing relevance, while timber production might have been important, even though not as intensive as in lower altitude Norway spruce forests of the same valley. In this regard, the circa 20-year long release-suppression cycles occurring in the early stand history hint at a utilization of the forest with a utilization frequency of the abovementioned length (Fig. 4). Therefore, we cannot formulate any hypothesis about harvest intensity and silvicultural principles used in the 18<sup>th</sup> and 19<sup>th</sup> century, but we cannot exclude similarities with selection cutting currently applied in several parts of the Alps. An additional hypothesis that could explain the dominance of Swiss stone pine is that during the last centuries, because of its resistance to weathering, larch timber was largely used for construction all over the Alps (Gambetta et al. 2004). Therefore, local foresters could have preferentially targeted European larch, felling large and mid-sized trees and hence making impossible to trace the establishment of this species back to the 19<sup>th</sup> century.

Besides historical reasons, the dominance of Swiss stone pine can be explained through ecological processes. For instance, the absence of events that significantly altered growth dynamics and species composition could have negatively affected European larch, as it demands high light availability and bare or disturbed soil to germinate, whereas a relatively undisturbed stand with cold aspect, as occurs in this study, allowed Swiss stone pine to establish easily (Li and Yang 2004). In addition, the dense rhododendron understory makes germination of species with light seeds, such as larch, quite difficult. For these reasons, the dominance of Swiss stone pine in the large trees layer seems to be the result of a synergic combination of ecological and human-

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

induced factors. On the other hand, small trees showed a more balanced species composition and a higher relative frequency of *Larix decidua* than the large trees population (Fig. 3). This could be due to higher frequency of small-scale disturbances, e.g. more frequent utilizations, that promoted the establishment of this pioneer species, at least until active forest management was carried on. In addition, both European larch and Swiss stone pine were able to endure growth suppression for a very long time, since individuals with dbh<7.5 cm and ages of 93 and 75 years have respectively been sampled. The ability to survive for several decades under forest canopy conditions is traditionally considered a trait of shade-tolerant species (Lorimer 1983), but these findings highlight how both European larch and Swiss stone pine may exhibit a higher ecological plasticity to this extent, also in light of the harsh environmental conditions experienced in subalpine forests which slowdown growth rates.

Establishment of the current large trees cohort was temporally limited to a time span of about 40 years (1885-1925). Moreover, the last harvesting in this area was carried out at the beginning of the 1960s. This was confirmed by a high frequency of tree establishment from 1955 to 1965 (Fig. 3). Larch budmoth outbreaks have been reported to occur in cycles 8-10 years apart (Baltensweiler and Fischlin 1988) and to [spread](#) eastwards starting from the Upper Engadine valley, following the predominantly westerly winds blowing through the Alpine arc (Baltensweiler and Rubli 1999). Consistently to our study, outbreaks have been registered in the eastern Alps (Büntgen et al. 2009) as well as in other areas of the Alpine region in the early 1950 (Price et al. 2006). In this regard, the most severe growth suppression we could detect was the one of European larch during the 1950 decade and the contemporary release of Swiss stone pine growth (Fig. 4). This event could be related to a larch budmoth outbreak. As a consequence of defoliation, larch experienced a strong and sustained reduction in growth, supported also by direct observation of tree-ring and latewood width, with an observed negative pointer year in 1953 followed by a circa 3-year period of reduced yearly and latewood growth (Baltensweiler et al. 2008). Swiss stone pine seems to have benefitted from the availability of resources made possible by the suppression of larch, showing a quasi-simultaneous increase in growth. However, the most important finding of this study is the lack of small trees establishment after 1970, coinciding with the cessation of active management occurred in 1966. Moreover, as pointed out by the growth dominance analysis (Fig. 5), the relevance of small and large trees in biomass production changed in the middle of 20<sup>th</sup> century favoring the latter, hinting at a changed contribution of the two classes, likely triggered by the interruption of forest management. Therefore, the absence of small-scale natural perturbations and silvicultural tending is leading to the reduction of suitable microsites for seed germination and saplings establishment of both species and consequently the stand is evolving towards a new phase characterized by a less heterogeneous age-structure.

[To this end, although they are pertaining only to the current state of the forest, results about spatial structure reinforce the previous considerations about changes in the stand structure.](#) Tree spatial pattern was clumped at all distances in both large and small trees, particularly for distances < 3 m (Figs. 1, ~~Fig. 6~~ and ~~Fig. 7~~). Aggregated patterns are typical of high-elevation subalpine forests and originate from facilitative processes in the regeneration phase (Brang et al. 2001, Motta and Lingua 2005). Trees tend to establish in groups, thus

obtaining mutual ecological advantages against strongly limiting environmental factors (wind, snow, erosion, etc.) (Callaway and Walker 1997). The feeding behavior of the Spotted nutcracker is a further cause of clumped spatial pattern for Swiss stone pine. Small trees of all species pooled exhibited a positive spatial association with the large trees population (Fig. 8a and 9a), confirming the preference for clumped patterns and the facilitative influence of large trees on regeneration processes. However, this outcome seems to depend on the dominance of Swiss stone pine also in the small trees layer, as the two species showed a different behavior when considered one at a time. In fact, while Swiss stone pine exhibited spatial association at short distances (Fig. 8b and 9b), larch regeneration occurred preferentially between 3 and 5 meters from large trees (Fig. 8c and 9c), confirming the light-demanding trait of this species and the preference for canopy gaps. Considering large trees only, Swiss stone pine exhibited a positive autocorrelation for age and height, whereas larch did not show positive autocorrelation for almost any of the distance lags of all the parameters (Fig. 10d, 10e, 10f). This suggests a different colonization strategy and/or competition experienced by the two species. Pine trees established more quickly after small-scale perturbations (individuals of similar age in a small space) and experienced a stronger competition (individuals of different diameter in a small space) than larch. The general positive age autocorrelation of large trees, especially Swiss stone pine, is contrasted by the absence of age autocorrelation of small trees (Fig. 10i). This discrepancy suggests that the formation of regeneration nuclei of the dominant species in the past has been faster than today. The long suppression period that small trees can tolerate is a likely explanation for the different age autocorrelation patterns between the large tree and small tree populations. Nevertheless, the absence of forest management in the last 50 years might have represented a crucial factor in determining the slowdown of the regeneration dynamics.

## Conclusions

Our study is one of the few studies showing how the lack of forest management caused the interruption of tree establishment and a potential homogenization of the structure, which could negatively affect the ability of this forest to provide services such as its potential protective role (Dorren et al. 2004). This highlights the importance of an active, sustainable management in maintaining a heterogeneous structure, with an uninterrupted recruitment of new individuals.

## Acknowledgements

We would like to acknowledge the Magnifica Comunità di Fiemme and its personnel for the authorization to carry out this study and for technical support during fieldwork. We express our gratitude to Prof. Pietro Piussi for his help in selecting the research plot. We acknowledge the editor and three anonymous referees for their valuable comments. We also thank Giuseppe Silvestro and Marco Ceccaroni for their contribution to this study through their degree thesis.

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

**References**

Bailey TC, Gatrell AC (1995) Interactive spatial data analysis. Longman Scientific and Technical Unlimited, Essex.

Baltensweiler W (1964) Zeiraphera griseana Hubner (Lepidoptera - Tortricidae) In European Alps - Contribution to problem of cycles. Can Entomol 96:792.

Baltensweiler W, Fischlin A (1988) The larch budmoth in the Alps. In: Dynamics of forest insect populations. Plenum Publishing Corporation, pp 331-351.

Baltensweiler W, Rubli D (1999) Dispersal: an important driving force of the cyclic population dynamics of the larch bud moth, Zeiraphera diniana Gn. Forest Snow and Landscape Research 74: 3-153.

Baltensweiler W, Weber UM, Cherubini P (2008) Tracing the influence of larch-bud-moth insect outbreaks and weather conditions on larch tree-ring growth in Engadine (Switzerland). Oikos 117:161–172. doi: 10.1111/j.2007.0030-1299.16117.x

[Binkley D, Olsson U, Rochelle R, Stohlgren T, Nikolov N. \(2003\) Structure, production and resource use in some old-growth spruce/fir forests in the front range of the Rocky Mountains, USA. For Ecol Manage. 172:271–279.](#)

Binkley D (2004) A hypothesis about the interaction of tree dominance and stand production through stand development. For Ecol Manage 190:265–271. doi: 10.1016/j.foreco.2003.10.018

[Blarquez O, Carcaillet C, Bremond L, Mourier B, Radakovitch O. \(2009\) Trees in the subalpine belt since 11 700 cal. BP: origin, expansion and alteration of the modern forest. The Holocene 20:139–146. doi: 10.1177/0959683609348857](#)

Brang P, Schönenberger W, Ott E (2001) Forests as protection from natural hazards. In: The Forest Handbook Vol. 2 (eds J Evans). Blackwell Science, Oxford.

[Brang P, Schönenberger W, Frehner M, Schwitter R, Wasser B. \(2006\) Management of protection forests in the European Alps : an overview. 44:23–44.](#)

[Büntgen U, Frank D, Liebhold A, Johnson D, Carrer M, Urbinati C, Grabner M, Nicolussi K, Levanic T, Esper J. \(2009\) Three centuries of insect outbreaks across the European Alps. New Phytol \[Internet\]. \[cited 2012 Jan 9\]; 182:929–41. doi: 10.1111/j.1469-8137.2009.02825.x](#)

Callaway RM, Walker LR (1997) Competition and facilitation: a synthetic approach to interactions in plant communities.. Ecology 78:1958–1965. doi: 10.1890/0012-9658(1997)078

Camarero JJ, Gutiérrez E, Fortin M-J (2000) Spatial pattern of subalpine forest-alpine grassland ecotones in the Spanish Central Pyrenees. For Ecol Manage 134:1–16. doi: 10.1016/S0378-1127(99)00241-8

Carrer M, Urbinati C (2001) Spatial analysis of structural and tree-ring related parameters in a timberline forest in the Italian Alps. J Veg Sci 12:643–652. doi: 10.2307/3236904

[Casalegno S, Amatulli G, Camia A, Nelson A, Pekkarinen A. \(2010\) Vulnerability of Pinus cembra L. in the Alps and the Carpathian mountains under present and future climates. For Ecol Manage 259:750–761. doi: 10.1016/j.foreco.2009.10.001](#)

- 397 Condit R, Ashton PS, Baker P, Bunyavejchewin S, Gunatilleke S, Gunatilleke N, Hubbell SP, Foster RB, Itoh A,  
398 LaFrankie JV, [et al.](#) (2000) Spatial patterns in the distribution of tropical tree species. *Science* 288: 1414-  
399 1418.
- 400 Cook ER (1985) A time series approach to tree-ring standardization. Dissertation, University of Arizona, Tucson,  
401 AZ.
- 402 Cook ER, Kairiukstis LA (1990) *Methods of Dendrochronology*. Kluwer, Dordrecht, The Netherlands.
- 403 Dale MRT (1999) *Spatial pattern analysis in plant ecology*, Cambridge University Press, Cambridge.
- 404 Diggle PJ (1983) *Statistical analysis of point patterns*. Academic Press, London.
- 405 [Dorren LK., Berger F, Imeson AC, Maier B, Rev F. \(2004\) Integrity, stability and management of protection](#)  
406 [forests in the European Alps](#). For Ecol Manage 195:165–176. doi: 10.1016/j.foreco.2004.02.057
- 407 Druckenbrod DL (2005) Dendroecological reconstructions of forest disturbance history using time-series  
408 analysis with intervention detection. *Can J For Res* 35:868–876.
- 409 Duncan RP (1991) Competition and the Coexistence of Species in a Mixed Podocarp Stand. *J Ecol* 79:1073. doi:  
410 10.2307/2261099
- 411 Ise T, Moorcroft PR (2008) Quantifying local factors in medium-frequency trends of tree ring records: Case  
412 study in Canadian boreal forests. For Ecol Manage 256:99–105.
- 413 Fernández ME, Tschieder EF, Letourneau F, Gyenge JE (2011) Why do Pinus species have different growth  
414 dominance patterns than Eucalyptus species? A hypothesis based on differential physiological plasticity.  
415 For Ecol Manage 261:1061–1068. doi: 10.1016/j.foreco.2010.12.028
- 416 Ferrari E (1988) La gestione dei boschi in provincia di Trento. *L'Italia Forestale e Montana*, Anno XLII, 6.
- 417 Fortin MJ, Dale MRT, Ver Hoef J (2002) Spatial analysis in ecology. In: *Encyclopedia of Environmetrics* (El-  
418 Shaarawi AH, Piegorsch WW eds). John Wiley and Sons Ltd, Chichester, pp 2051-2058.
- 419 Frey W (1983) The Influence of Snow on Growth and Survival of Planted Trees. *Arct Alp Res* 15:241. doi:  
420 10.2307/1550925
- 421 Fritts HC, Mosimann JE, Bottorff CP (1969) A revised computer program for standardizing tree-ring series.  
422 *Tree-Ring Bulletin* 29: 15-20.
- 423 Fritts HC (1976) *Tree rings and climate*. Academic Press, London.
- 424 Gambetta A, Susco D, Zanuttini R (2004) Determination of the natural durability of larch wood (*Larix decidua*  
425 Mill.) from the Western Italian Alps. *Holzforschung* 58:678–681. doi: 10.1515/HF.2004.123
- 426 Garbarino M, Lingua E, Martinez Subirà M, Motta R (2011) The larch wood pasture: structure and dynamics of  
427 a cultural landscape. *Eur J For Res* 130:491–502. doi: 10.1007/s10342-010-0437-5
- 428 [Genries A, Muller SD, Mercier L, Bircker L, Carcaillet C. \(2009\) Fires Control Spatial Variability of Subalpine](#)  
429 [Vegetation Dynamics During the Holocene in the Maurienne Valley \(French Alps\)](#). *Ecoscience* 16:13–22.  
430 doi: 10.2980/16-1-3180
- 431 Gignoux J, Duby C, Barot S (1999) Comparing the performances of Diggle's test of spatial randomness for small  
432 samples with and without edge-effect correction: application to ecological data. *Biometrics* 55:156-164.



1  
2  
3 433 Haase P (1995) Spatial pattern-analysis in ecology based on Ripley K function – introduction and methods of  
4 434 edge correction. *Journal of Vegetation Science* 4:575–582.  
5  
6 435 Holtmeier F-K (2009) The Borealis. The future of northern forests. *ERDE* 140:126–126.  
7  
8 436 Krüsi BO, Moser B (2000) Impacts of snow and ungulates on the successional development of a mountain pine  
9 437 stand in the Swiss National Park (Munt La Schera). In: Schütz M, Krüsi BO, Edwards PJ (eds) *Succession*  
10 438 *research in the Swiss National Park. Nationalpark-Forschung in der Schweiz* 89: 176–197.  
11  
12 439 Li M-H, Yang J (2004) Effects of microsite on growth of *Pinus cembra* in the subalpine zone of the Austrian Alps.  
13 440 *Ann For Sci* 61:319–325. doi: 10.1051/forest:2004025  
14  
15 441 Lingua E, Cherubini P, Motta R, Nola P (2008) Spatial structure along an altitudinal gradient in the Italian  
16 442 central Alps suggests competition and facilitation among coniferous species. *J Veg Sci* 19:425–436. doi:  
17 443 10.3170/2008-8-18391  
18  
19 444 Lorimer C (1983) A test of the accuracy of shade-tolerant classifications based on physiognomic and  
20 445 reproductive traits. *Can J Bot* 61:1595–1598.  
21  
22 446 Lorimer CG (1985) Methodological considerations in the analysis of forest disturbance history. *Can J For Res*  
23 447 15:200–213. doi: 10.1139/x85-038  
24  
25 448 Lotwick H, Silverman B (1982) Methods for analyzing spatial processes of several types of points. *J R Stat Soc*  
26 449 *Ser B-METHODOLOGICAL* 44:406–413.  
27  
28 450 Meyer HA (1943) Management without rotation. *Journal of Forestry* 41: 126-132.  
29  
30 451 Moeur M (1993) Characterizing spatial patterns of trees using stem-mapped data. *For Sci* 39:756–775.  
31  
32 452 Moran PAP (1950) Notes on Continuous Stochastic Phenomena. *Biometrika* 37:17. doi: 10.2307/2332142  
33  
34 453 Motta R, Nola P, Piussi P (1999) Structure and stand development in three subalpine Norway spruce (*Picea*  
35 454 *abies* (L.) Karst.) stands in Paneveggio (Trento, Italy). *Glob Ecol Biogeogr* 8:455–471. doi: 10.1046/j.1365-  
36 455 2699.1999.00165.x  
37  
38 456 Motta R, Lingua E (2005) Human impact on size, age, and spatial structure in a mixed European larch and Swiss  
39 457 stone pine forest in the Western Italian Alps. *Can J For Res* 35:1809–1820. doi: 10.1139/x05-107  
40  
41 458 Nola P, Morales M, Motta R, Villalba R (2006) The role of larch budmoth (*Zeiraphera diniana* Gn.) on forest  
42 459 succession in a larch (*Larix decidua* Mill.) and Swiss stone pine (*Pinus cembra* L.) stand in the Susa Valley  
43 460 (Piedmont, Italy). *Trees* 20:371–382. doi: 10.1007/s00468-006-0050-x  
44  
45 461 Perry GLW (2004) SpPack: spatial point pattern analysis in Excel using Visual Basic for Applications (VBA).  
46 462 *Environmental Modelling & Software* 19:559-569.  
47  
48 463 Pfeifer K, Kofler W, Oberhuber W (2005) Climate related causes of distinct radial growth reductions in *Pinus*  
49 464 *cembra* during the last 200 yr. *Veg Hist Archaeobot* 14:211–220. doi: 10.1007/s00334-005-0001-2  
50  
51 465 Price B, Allgöwer B, Fischlin A (2006) Synchrony and travelling waves of larch bud moth? Time series analysis  
52 466 with changing scale. *Ecol Modell* 199:433–441. doi: 10.1016/j.ecolmodel.2005.11.048  
53  
54 467 Provincia Autonoma di Trento (2013) Progetto di attuazione della rete di riserve Fiemme-Destra Avisio.  
55 468 Provincia Autonoma di Trento, Trento.  
56  
57  
58  
59  
60



- 469 Renshaw E (2009) Spatial-temporal marked point processes: a spectrum of stochastic models. *Environmetrics*  
470 21:253–269.
- 471 Ridolfi L (2009) Metodi di studio delle dinamiche strutturali delle foreste e indagini preliminari svolte in una  
472 cembreta in Val di Fiemme. Bachelor Degree Thesis, Università di Bologna.
- 473 Ripley B (1977) Modeling spatial patterns. *J R Stat Soc Ser B-Methodological* 39:172–212.
- 474 Ripley B (1979) Tests of randomness for spatial point patterns. *J R Stat Soc Ser B-Methodological* 41:368–374.
- 475 [Risch AC, Nagel LM, Schutz M, Krusi BO, Kienast F, Bugmann H. \(2003\) Struktur und Langzeitentwicklung von](#)  
476 [subalpinen \*Pinus montana\* Miller und \*Pinus cembra\* L. Waldern in den zentraleuropäischen Alpen.](#)  
477 [Forstwissenschaftliches Cent 122:219–230. doi: 10.1046/j.1439-0337.2003.03011.x](#)
- 478 Rubino D, McCarthy B (2004) Comparative analysis of dendroecological methods used to assess disturbance  
479 events. *Dendrochronologia* 21:97–115. doi: 10.1078/1125.7865.00047
- 480 Schloeth R (1998) Die Lärche: ein intimes Baumporträt. 2nd Edition. AT Verlag, Aarau.
- 481 Schönenberger, W. 1985. Performance of a high altitude afforestation under various site conditions. In  
482 Establishment and Tending of Subalpine Forest: Research and Management. Eds. H. Turner and W.  
483 Tranquillini. Proc. 3rd IUFRO Workshop. Eidg. Anst. forstl. Versuchswes., Berlin 210: 233-240.
- 484 Scrinzi G, Galvagni D, Marzullo L (2010) I nuovi modelli dendrometrici per la stima delle masse assestamentali  
485 in provincia di Trento. Provincia Autonoma di Trento, Servizio Foreste e Fauna.
- 486 Shimatani IK, Kubota Y (2011) The spatio-temporal forest patch dynamics inferred from the fine-scale  
487 synchronicity in growth chronology. *J Veg Sci* 22:334–345.
- 488 Tinner W, Kaltenrieder P (2005) Rapid responses of high-mountain vegetation to early Holocene  
489 environmental changes in the Swiss Alps. *J Ecol* 93:936–947. doi: 10.1111/j.1365-2745.2005.01023.x
- 490 [Tonon G, Panzacchi P, Grassi G, Gianfranco M, Cantoni L, Bagnaresi U. \(2005\) Spatial dynamics of late](#)  
491 [successional species under \*Pinus nigra\* stands in the northern Apennines \(Italy\). \*Ann For Sci\* 62:669–679.](#)  
492 [doi: 10.1051/forest:2005059](#)
- 493 [Tranquillini W. 1979. \*Physiological Ecology of the Alpine Timberline\*. Berlin, Heidelberg: Springer Berlin](#)  
494 [Heidelberg.](#)
- 495 [Veblen TT, Hadley KS, Nel EM, Kitzberger T, Reid M, Villalba R. \(1994\) \*Disturbance Regime and Disturbance\*](#)  
496 [Interactions in a Rocky Mountain Subalpine Forest.](#) *J Ecol* 82:125. doi: 10.2307/2261392
- 497 Wolynski A, Zanin M, Scrinzi G (2009). Revisione della pianificazione forestale in Trentino a cinquant'anni  
498 dall'adozione della selvicoltura naturalistica. Atti del III Congresso Nazionale di Selvicoltura, Taormina 15-  
499 18 ottobre 2008, pp. 928-932.
- 500 [Wunder J, Brzeziecki B, Zybura H, Reineking B, Bigler C, Bugmann H. \(2008\) Growth-mortality relationships as](#)  
501 [indicators of life-history strategies: a comparison of nine tree species in unmanaged European forests.](#)  
502 [OIKOS](#) 117:815–828. doi: 10.1111/j.2008.0030-1299.16371.x

503

504 **Tables captions**

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

**Table 1** Species mixture, total basal area and stand characteristics of the 1-ha area. Absolute values and relative abundance (%) referred to both small (DBH<7.5 cm) and large trees populations (DBH>7.5 cm). Stand characteristics referred to large trees population only.  $g_m$ : average basal area;  $h_{mg}$ : height at average basal area diameter;  $Hd$ : dominant height (average height of the tallest 100 large trees);  $d_{mg}$ : diameter at average basal area;  $V$ : standing volume

**Figure captions**

**Figure 1** Mapped spatial distribution of both small and large trees of all species within the 1-ha plot. The 25 trees of Swiss stone pine and European larch that were used for the growth release/suppression analysis are highlighted with thick dark borders. PIAB\_L: large Norway spruce; PICE\_L: large Swiss stone pine; LADE\_L: large European larch; SOAU\_L: large European rowan; PIAB\_S: small Norway spruce; PICE\_S: small Swiss stone pine; LADE\_S: small European larch; SOAU\_S: small European rowan; PICE\_sel: Swiss stone pine trees selected for growth release/suppression analysis; LADE\_sel: European larch trees selected for growth release/suppression analysis.

**Figure 2** Diameter (a) and height class (b) distribution of large and small trees. In (a) all small trees have been included in one single class with dbh<7.5 cm. PICE = *Pinus cembra*; LADE = *Larix decidua*; PICE\_S = *Pinus cembra* small trees; PICE\_S = *Larix decidua* small trees.

**Figure 3** Age structure of the studied stand showed in 5-years interval classes. Large trees (*large*) and small trees (*small*) of both species have been represented separately. PICE = *Pinus cembra*; LADE = *Larix decidua*.

**Figure 4** Frequency of growth release and growth suppression periods in PICE = *Pinus cembra* and LADE = *Larix decidua*. The frequency represents the percentage of trees showing growth releases/suppressions among the whole sample. Secondary y axis: number of trees implemented in the sample.

**Figure 5** Growth dominance analysis chart. In the upper part is the amount of trees implemented in the sample. In the lower part the GD (growth dominance) trend (continuous line) and single values (dots) over time.

**Figure 6** Univariate point pattern analysis of large and small trees pooled, and Swiss stone pine and European larch separately.  $L(d)$  square root transformation is shown (continuous line), with a 99% Monte Carlo confidence envelope (dashed line). PICE = *Pinus cembra*; LADE = *Larix decidua*.

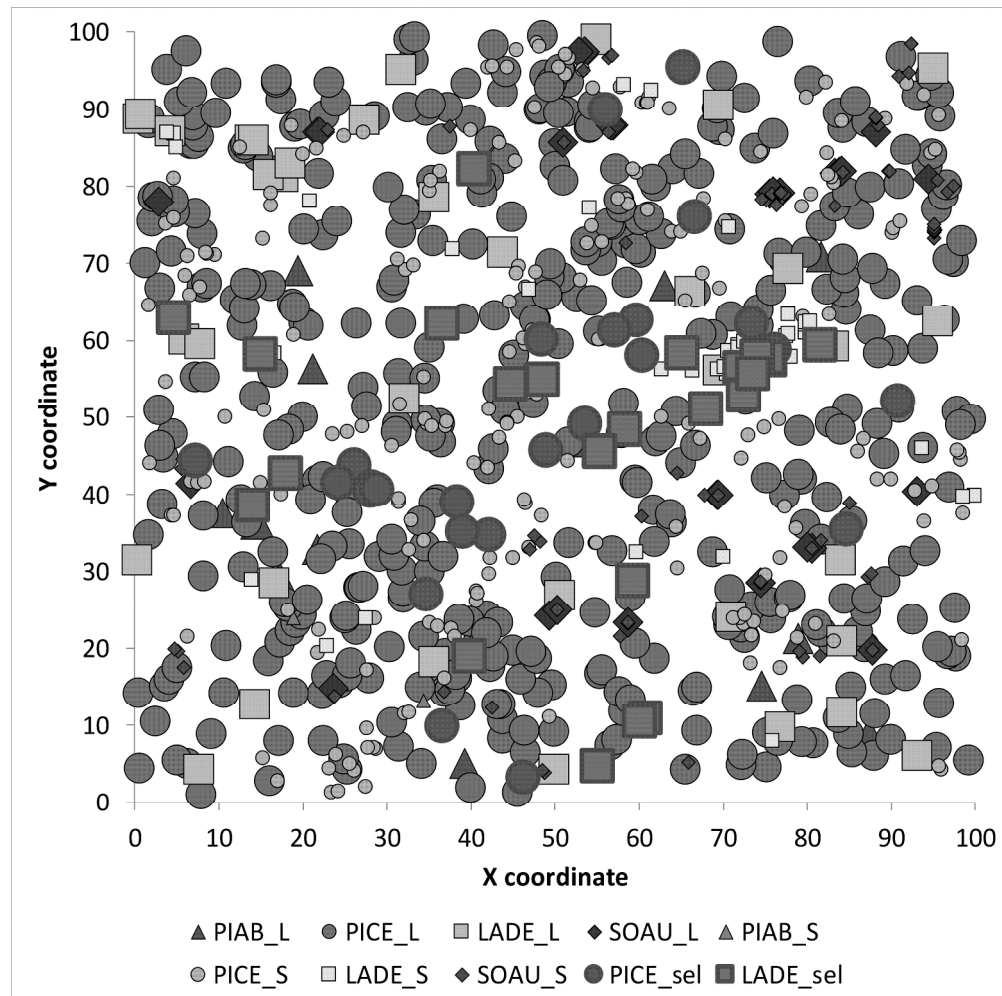
**Figure 7** Diggle's G function analysis for large and small trees pooled, and Swiss stone pine and European larch separately.  $G(w)$  is shown (continuous line), with a 99% Monte Carlo confidence envelope (dashed line). PICE = *Pinus cembra*; LADE = *Larix decidua*.

536 **Figure 8** Bivariate point pattern analysis: between large trees and small trees (pooled); intra-specific for Swiss  
537 stone pine and European larch separately; inter-specific comparing large trees and small trees of both species  
538 separately. Square root transformation  $L_{12}(d)$  is shown (continuous line), with a 99% Monte Carlo confidence  
539 envelope (dashed line). PICE = *Pinus cembra*; LADE = *Larix decidua*.

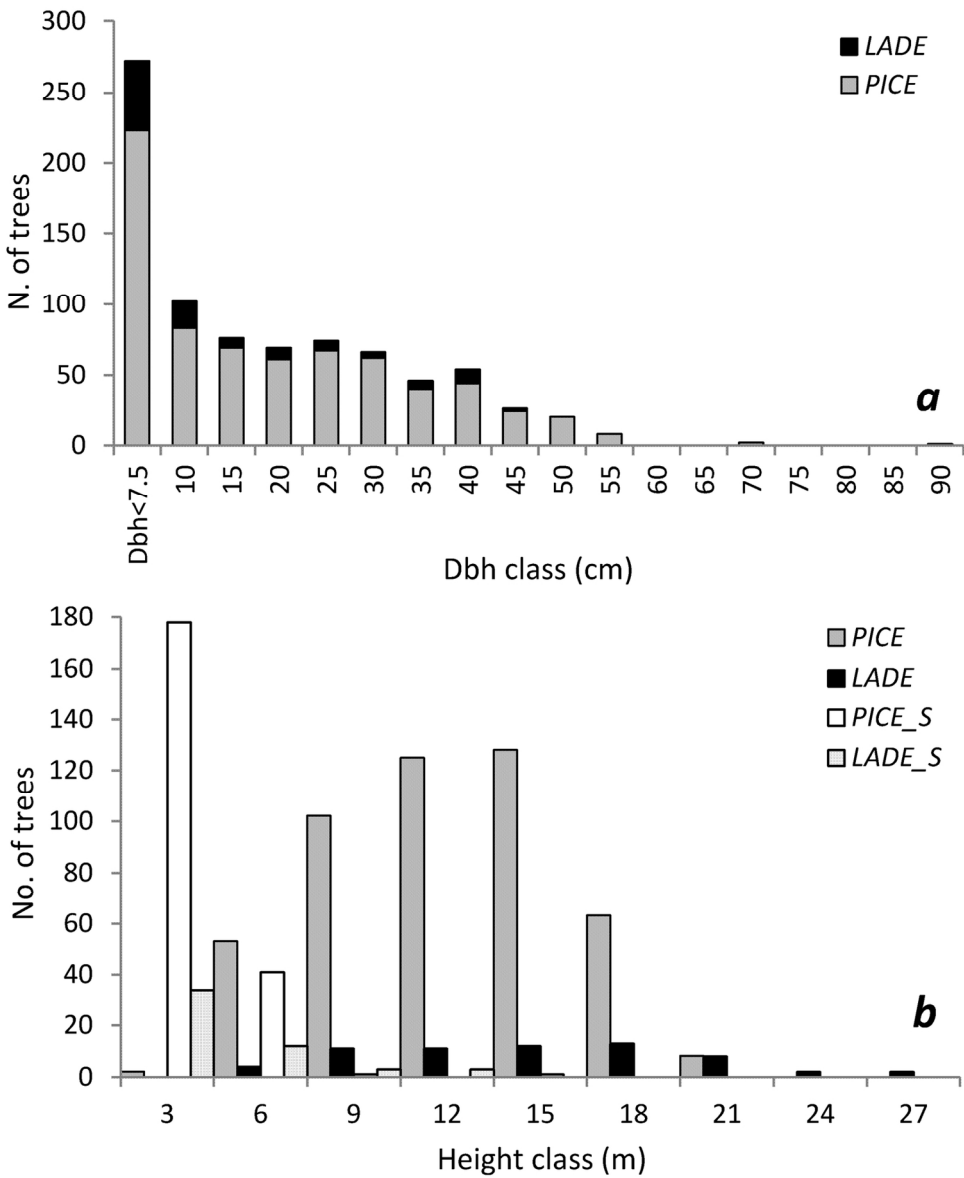
540 **Figure 9** Relative neighborhood density between large trees and small trees (pooled); intra-specific for Swiss  
541 stone pine and European larch separately; inter-specific comparing large trees and small trees of both species  
542 separately. Relative neighborhood density is shown (continuous line), with a 99% Monte Carlo confidence  
543 envelope (dashed line). PICE = *Pinus cembra*; LADE = *Larix decidua*.

544 **Figure 10** Moran's I correlograms for diameter, height and age of large and small trees (pooled) and Swiss  
545 stone pine and European larch separately. Double-sized markers: spatial autocorrelation significant at  $P < 0.05$ .  
546 PICE = *Pinus cembra*; LADE = *Larix decidua*.

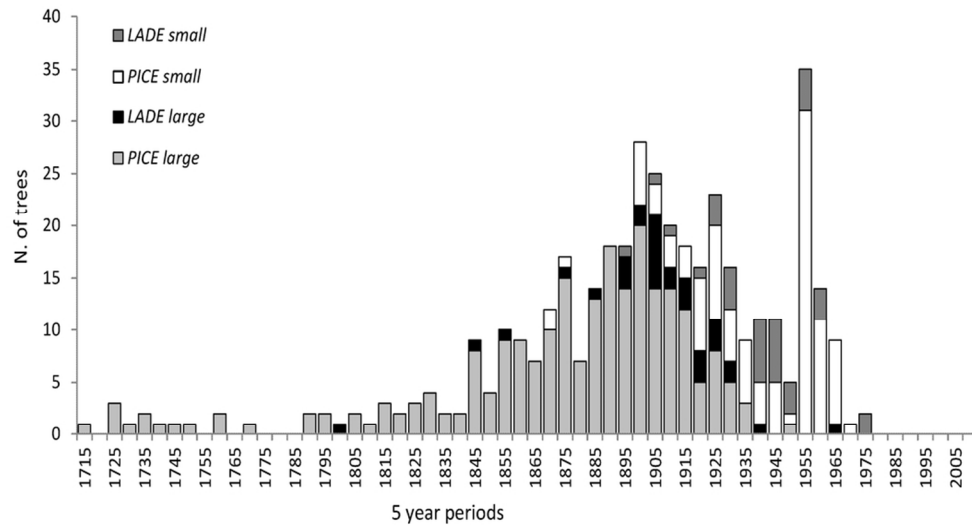
	Large trees	Small trees	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Stand characteristics	
<i>P. cembra</i>	481 (81%)	224 (60%)	31.50 (86%)	<b><i>g<sub>m</sub></i> (m<sup>2</sup> ha<sup>-1</sup>)</b>	0.06
<i>L. decidua</i>	63 (11%)	49 (13%)	3.22 (9%)	<b><i>h<sub>mg</sub></i> (m)</b>	13.37
<i>S. aucuparia</i>	34 (6%)	96 (26%)	0.23 (1%)	<b><i>Hd</i> (m)</b>	18.58
<i>P. abies</i>	15 (2%)	2 (1%)	1.60 (4%)	<b><i>d<sub>mg</sub></i> (cm)</b>	27.63
Total	593	371	36.55	<b><i>V</i> (m<sup>3</sup> ha<sup>-1</sup>)</b>	253.89



229x228mm (300 x 300 DPI)

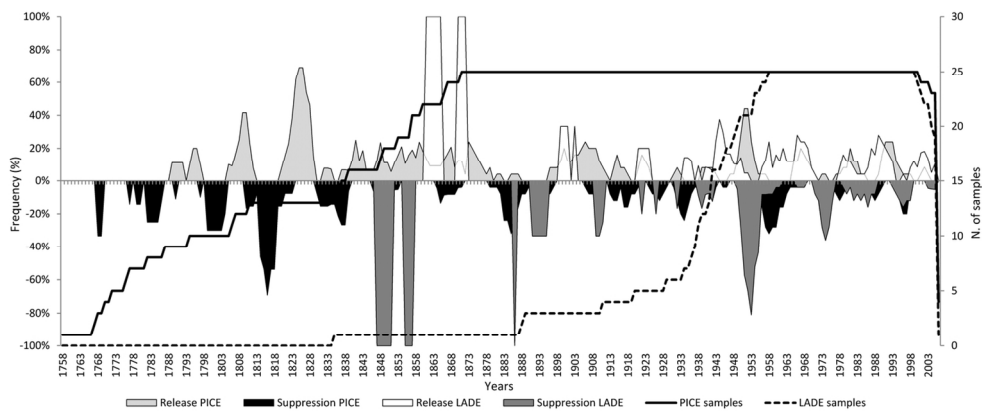


143x170mm (300 x 300 DPI)

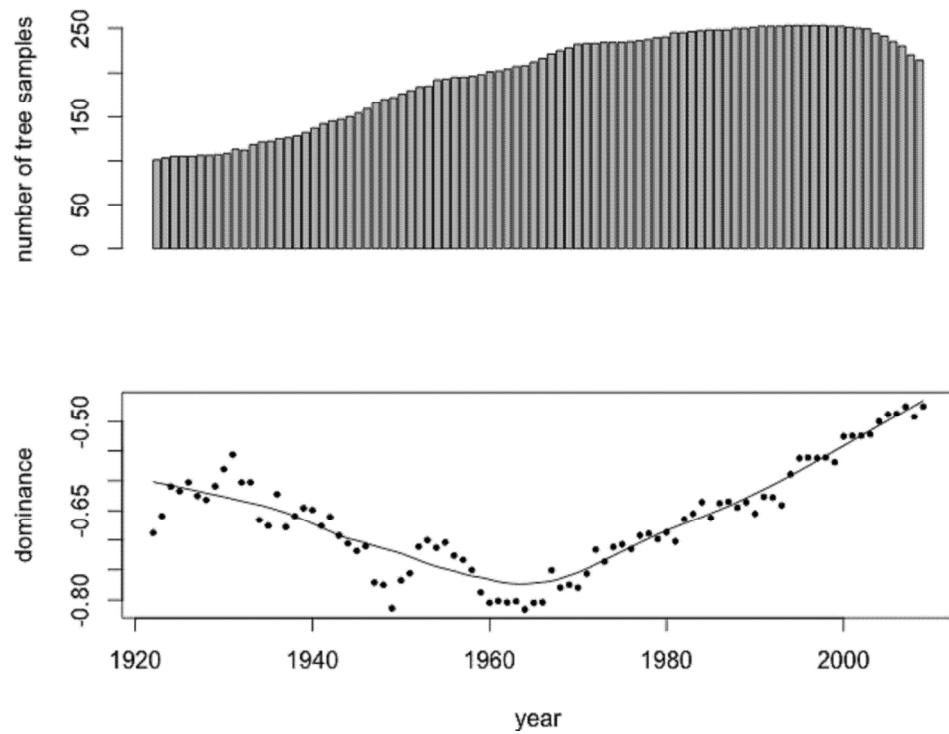


91x48mm (300 x 300 DPI)

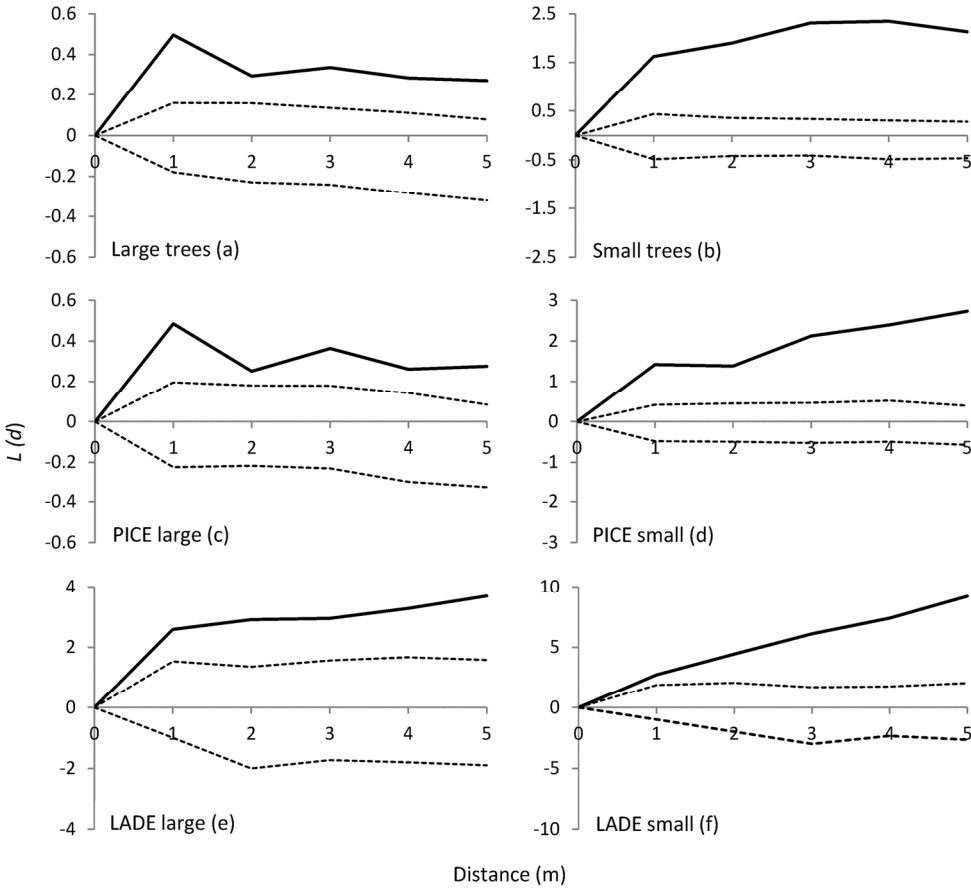




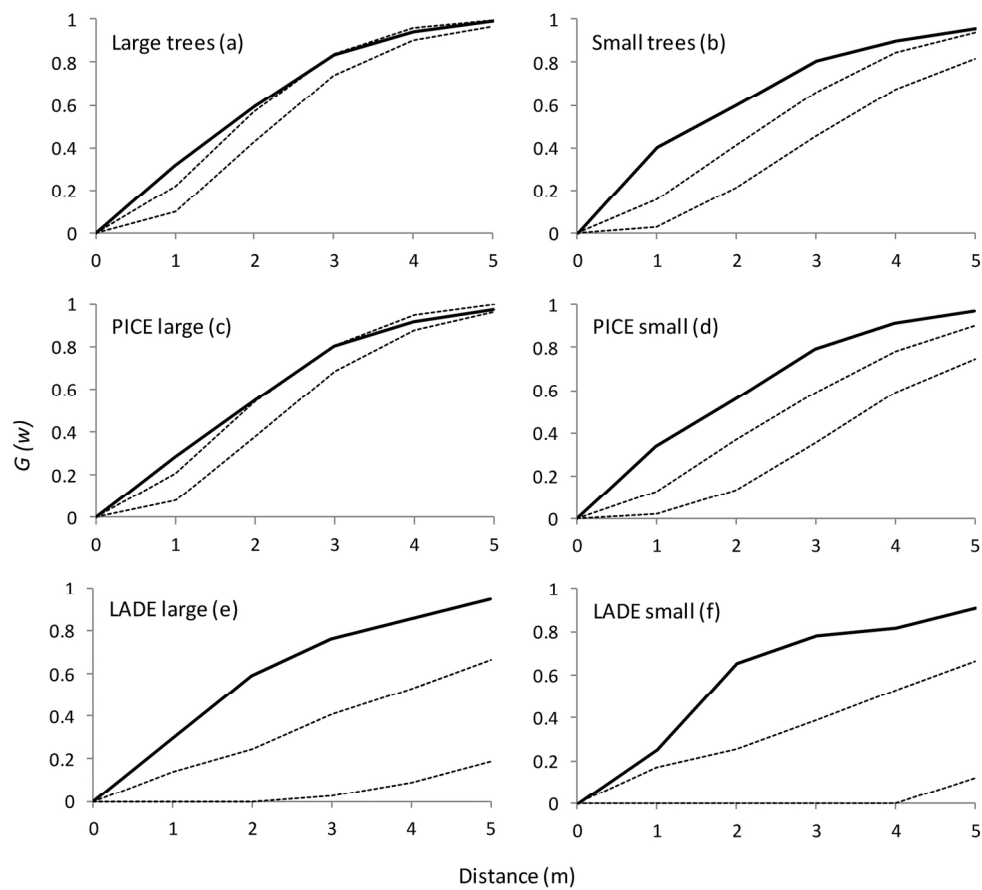
128x55mm (300 x 300 DPI)



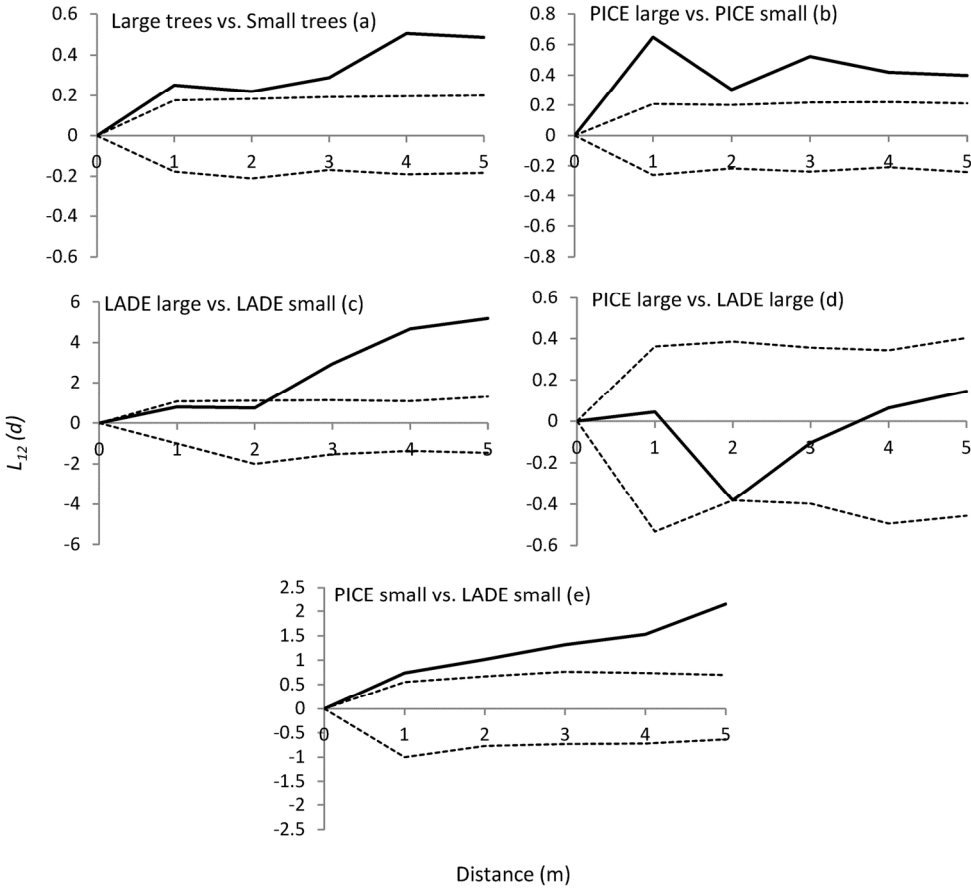
127x93mm (300 x 300 DPI)



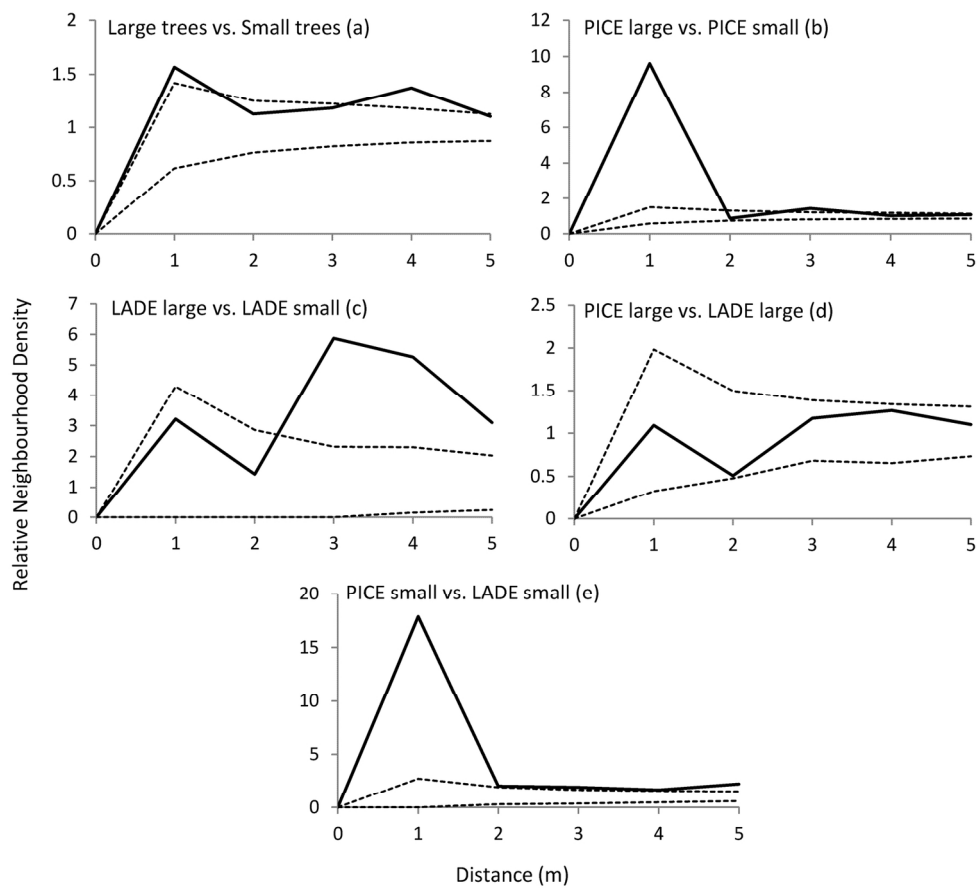
156x141mm (300 x 300 DPI)



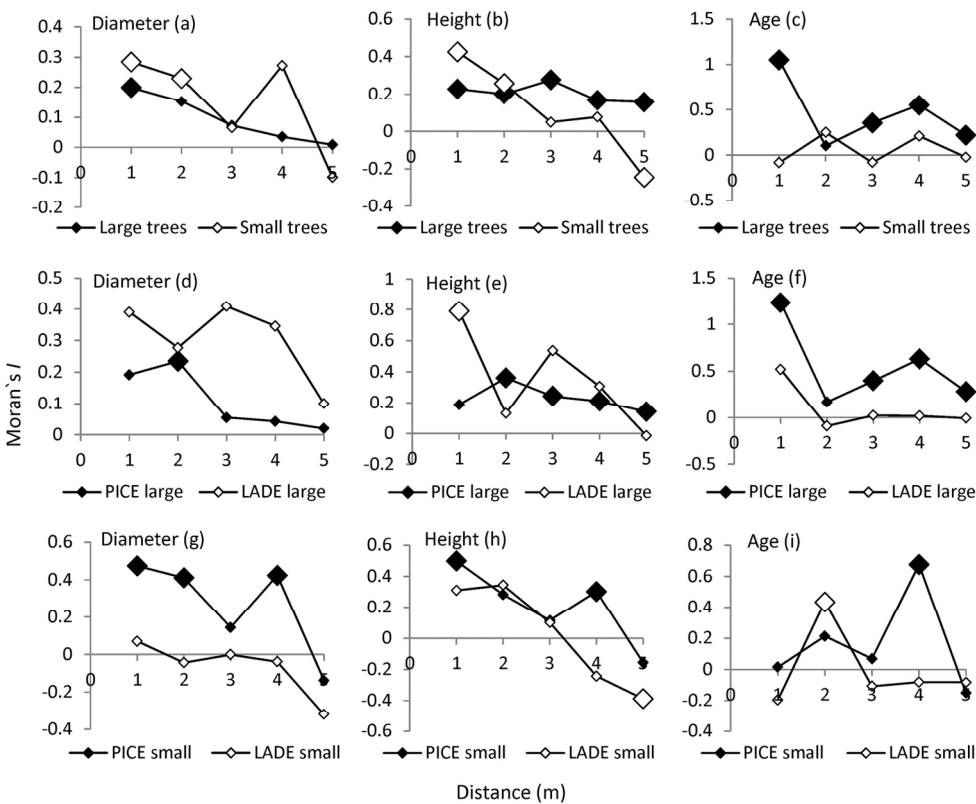
156x139mm (300 x 300 DPI)



156x141mm (300 x 300 DPI)



156x139mm (300 x 300 DPI)



141x115mm (300 x 300 DPI)